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*"Redescription of the African Fresh-water Crab
Sudanonautes Africanus"*

Neil Cumberlidge
Northern Michigan University

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REDESCRIPTION OF THE AFRICAN FRESH-WATER CRAB
SUDANONAUTES AFRICANUS (A. MILNE EDWARDS, 1869)
(BRACHYURA: POTAMOIDEA: POTAMONAUTIDAE)

Neil Cumberlidge

ABSTRACT

The African fresh-water crab *Sudanonautes africanus* (A. Milne Edwards, 1869) is redescribed from a large series of specimens from 5 countries. The species is redefined by a combination of characters of the carapace, chelipeds, and gonopod 1. The distribution of *S. africanus* is revised to include the coastal rain-forest regions of Nigeria and Central Africa (from south Cameroon to lower Zaire), and to exclude the West African region west of the river Niger in Nigeria. *Sudanonautes africanus* is one of the second intermediate hosts of the human lung fluke (*Paragonimus*).

The African fresh-water crab *Sudanonautes africanus* (A. Milne Edwards, 1869) is one of three species of *Sudanonautes* Bott, 1955, that were recognized by Bott (1955, 1959, 1964) and by Monod (1977, 1980). Since then, several other species have been assigned to this genus (Cumberlidge, 1991, 1993a, b, 1995).

Bott (1955) established the genus *Sudanonautes* (type species by original designation, *Thelphusa africana* A. Milne Edwards, 1869), and recognized two subgenera, *Sudanonautes sensu stricto*, and *Convexonautes* Bott, 1955 (type species by original designation, *Thelphusa aubryi* H. Milne Edwards, 1853). Until recently, three subspecies were assigned to *Sudanonautes* (*Sudanonautes*) *africanus*, namely *S. (S.) a. africanus* (A. Milne Edwards, 1869), *S. (S.) a. chaperi* (A. Milne Edwards, 1887), and *S. (S.) a. chavanesii* (A. Milne Edwards, 1886) (Bott, 1955, 1959; Monod, 1977, 1980). Cumberlidge (1985) subsequently referred *S. (S.) a. chaperi* to the genus *Liberonautes* Bott, 1955. *Sudanonautes africanus chavanesii* (A. Milne Edwards, 1886) should also be regarded as a valid species (Cumberlidge, 1995).

Correct identification of *S. africanus* is important, since this species, and three others—*S. aubryi* (H. Milne Edwards, 1853), *S. floweri* (de Man, 1901), and *S. granulatus* (Balss, 1929)—are second intermediate hosts of the human lung fluke *Paragonimus* in Nigeria and Central Africa (Voelker *et al.*, 1975; Voelker and Sachs, 1977; Nozais *et al.*, 1980). However, the ambiguous descriptions of these species in the literature (Bott, 1955; Monod, 1977, 1980) have led

to *S. africanus* being wrongly identified as *S. aubryi* (see Voelker and Sachs, 1977, fig. 1). *Sudanonautes aubryi* has also been wrongly identified as *S. africanus* in a number of other works (Bott, 1959; Lutz, 1969; Ejike, 1972; Voelker *et al.*, 1975, fig. 6; Monod, 1977, 1980; Bertrand, 1979).

Findings are presented here based upon the structure of the entire adult male gonopods of *S. africanus*, together with other characters of the mandibles, carapace, and chelipeds (Figs. 1a-j, 2a-i). Before the present study, there were no satisfactory figures of gonopods 1 and 2 of adults this species. The specimen used by A. Milne Edwards (1869) to describe *Thelphusa africana* was a small juvenile (CW 17 mm), while his more detailed description (A. Milne Edwards, 1887) was based on a larger, but still immature, female (CW 53 mm). Other early workers either did not describe the gonopods of *S. africanus* (see de Man, 1903; Rathbun, 1905; Balss, 1929), or only those of immature specimens (Capart, 1954). While Bott (1955) described the gonopods of an adult specimen of *S. africanus*, he sketched only the terminal segments. Finally, Monod's (1977, figs. 93-95, 102) illustrations of the gonopods of "*S. africanus*" from Togo are, in fact, those of *S. aubryi*. *Sudanonautes africanus* is redescribed on the basis of characters of the gonopods, carapace, sternum, chelipeds, and mandibles.

MATERIALS AND METHODS

Types. — The type specimen (MNHN) is a juvenile (CW 17, CL 13) and is in poor condition. It was collected from Gabon by M. Aubry-Lecomte. The female type

(MNHN) (CW 53, CL 39) was collected from the river Ogoué, Congo (=Gabon). A. Milne Edwards did not fix holotypes, so these specimens are syntypes. Neither is suitable to select as a lectotype, since one is a juvenile, and the other an immature female; therefore, no gonopods and mature chelipeds of the types are available. No topotypes are available. There are, however, several external features which are unique to this species that allow conspecific specimens to be selected. These characters include a small epibranchial tooth (about half the size of the intermediate and exorbital teeth), a large intermediate tooth as big as the exorbital tooth, a smooth untoothed anterolateral margin behind the epibranchial tooth, a very flat carapace (CH/CL = 0.43), patches of raised circular blisters and fields of raised short lines on the posterior surface of the carapace in the cardiac and branchial regions, and very deep semicircular, cardiac, and urogastric grooves. The species is redescribed here from an adult male (CW 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983), and an adult female (CW 108 mm) from a tributary of the river Ikpan, Cross River State, Nigeria (NMU 5.IV.1983).

Methods.—The left mandible and left gonopods 1 and 2 are illustrated (Fig. 2a–i). Four measurements, carapace length, carapace width, carapace height, and front width, were recorded from each specimen using digital calipers. Carapace proportions were calculated according to carapace length. These data were pooled and used for descriptions of growth (Fig. 3a, b). Statistical comparisons between species were made between sexually mature adults only (Table 1). The distribution of *S. africanus* described here is based on data from the direct examination of a large number of specimens from 60 different localities in 5 countries, since literature records are not reliable.

The following abbreviations are used: AMNH, American Museum of Natural History, New York, New York, U.S.A.; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHM, The Natural History Museum, London, United Kingdom; NNH, Natuurhistorisch Museum, Leiden, The Netherlands; NMU, Northern Michigan University, Marquette, Michigan, U.S.A.; RCM, Royal Congo Museum, Tervuren, Belgium; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; ZIM, Zoological Institute and Museum, Hamburg, Germany; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; CW = carapace width at widest point; CL = carapace length, measured along median line; CH = cephalothorax height, maximum height of cephalothorax; FW = front width, width of front measured along anterior margin, M = male, F = female, juv = juvenile.

TAXONOMY

Sudanonautes africanus (A. Milne Edwards, 1869)

Figs. 1a–j, 2a–i, 3a,b

Thelphusa africana A. Milne Edwards, 1869: 186, pl. XI, fig. 2, 2a, b; A. Milne Edwards, 1887: 124–126, pl. IV, fig. 8.

Potamon (Potamonautes) africanus, de Man, 1903: 41, pl. IX, figs. 7–9; Rathbun, 1904, pl. 16, fig. 6; Rathbun, 1905: 188–190, fig. 47; Balss, 1929: 124, 125, figs. 5–7; Balss, 1936: 166.

Potamon (Potamonautes) africanum, Colosi, 1920: 34; Colosi, 1924: 21, fig. 16; Roux, 1927: 237.

Potamon africanus, Chace, 1942: 204; Capart, 1954: 824, figs. 1, 6.

Sudanonautes (Sudanonautes) africanus africanus, Bott, 1955: 295–298, figs. 61, 93–95, 103 a–d, pl. XXVI, figs. 2a–c, 3; Bott, 1959: 1004, 1005; Monod, 1977: 1216, (not figs. 93–95, 102); Monod, 1980: 384, pl. V, fig. 27.

Material Examined.—NIGERIA: NNH 31552, 1 F adult, near Ogoja, about 6°40'N, 8°45'E, Ogatike, 22 Jan 1977, donated by C. B. Powell. NNH 31618, several juveniles, Tussen creek, Eagle Island, west of the College of Science & Technology, Port Harcourt, 30 Jan 1977, donated by C. B. Powell. NMU 12.5.1978, 1 F, juv (CW 34 mm), 1 M, juv (CW 21.5 mm), near Ekong on MCC road, temporary stream over sand, collected by J. C. Reid. NMU 29.IV.1979, 1 F (CW 90 mm), bearing > 100 hatchling crabs, small sample of many under abdomen. MCC = Akansoko road km 30, Calabar, Cross River State, 1400 h, permanent stream on southwest side of road. Crab extracted from burrow (not crevice) in about 20-cm deep fast moving water dropping from top of culvert. Burrow about 40 cm long and 9–10 cm wide, in mudstone/clay, collected by J. C. Reid. NMU 1.XI.1979, 1 F, immature (CW 45 mm), MCC = Akansoko road km 27, Calabar, Cross River State, 1600 h, mudstone stream bed, between culvert under road and first tributary to left as face downstream, no vegetation in that section of the stream, collected by J. C. Reid. NMU 4.IV.1983, 2 juv, remains incomplete, (CWs 57, 42 mm), Ekong road km 29, Cross River State, from standing water in a culvert, collected by J. C. Reid. NMU 5.IV.1983, 2 juv, (CWs 30, 17 mm), approximately 85 km NE of Calabar, small stream in palm oil estate on road to Ekang, Cross River State, downstream of bridge over river Ikpan, or one of its tributaries, slow flow over much rounded pale grey stones, edge of burnt plantation forest, collected by J. C. Reid. NMU 5.IV.1983, 1 F adult (CW 108 mm) with many live young under abdomen, tributary of river Ikpan, 80–90 km northeast of Calabar on the Ekang-Mamfe road, Cross River State, caught by hand at dawn at edge of slow-flowing stream (river Ayip), stream on grey soil, caught between log and cliff edge, turbid water, crab with claws and abdomen drooping (as if dead or suspended), possibly letting hatchlings near water, collected by N. Cumberlidge. NMU 9.IV.1983, 10 M, 9 F, 9 juv, stream at foot of Obudu plateau, Cross River State, stream dammed and bed drained, collected by N. Cumberlidge. CAMEROON: MCZ, 1 F juv (CW 31.5 mm), river Mbové at Edéa, 14 Apr 1971, collected by T. Roberts. MNHN B5024, 12 juv, Nkongsamba. NHM, 1902.8.16.2, 1 adult, Kribi river, south Cameroon. NHM 1907.7.1–5, 5 specimens, in forest 25 km east of Kribi. NHM, 1912.6.22, 1 adult, Bitye Ja river, south Cameroon, collected by G. L. Bates. NHM 1936.2.27.1–3, 3 M, immature, (CWs 65, 35, 34 mm), Batouri district. NHM 1938.7.1.1–15, 1 M adult (CW 115.3 mm), Mamfe, collected by I. Sanderson. NHM 1959.5.4 (18–19), 1 juv, Kumba. NNH 18409, 1 F immature, (CW 70

mm), collected by Prof. Dr. Vogel, 1963. NNH 21135, 3 large adults, 5 km southwest of N'Kilbissan, 18 May 1964, collected by B. De Wilde-Duyfjes. NNH 21155, 1 F immature, (CW 73 mm), about 10 km southeast of Amban, Mar 1964, collected by B. De Wilde-Duyfjes. NNH 21643, 1 M adult, N'Kilbissan, 24 Feb 1964, collected by B. De Wilde-Duyfjes. NNH 21644, 1 F adult, Kwoemvong, about 15 km south west of Ebolowa, 4 Mar 1964, collected by B. De Wilde-Duyfjes. NNH 21855, 1 M adult, about 40 km northwest of Eséka, 31 Mar 1964, collected by B. De Wilde-Duyfjes. NMU 1982, 15 juv, Kumba, collected by N. Cumberlandidge. RCM 46.960, 1 specimen, Thysville, 1956. RCM 51.555, 1 M adult (CW 82.4 mm), Muila, 8/9 Oct 1964, collected by Thijs van den Audenaerde. RCM 51.782, 1 adult, Makau, river Koukoup, 2 Oct 1965, collected by J. P. Omgba. RCM 51.783, several juv, Olokoe village, 20 Oct 1965, collected by J. P. Omyba. RCM 53.049, 1 specimen, river Lobé, 1 Oct 1968, collected by J. Van Mol. RCM 53.388, 6 specimens, Olounou, 11–19 Sep 1974, collected by F. Puylaert. RCM 53.392, 9 juv (CWs 10–33 mm), Olounou, 11–19 Sep 1971, collected by F. Puylaert. RCM 54.168, 1 adult, km 60 road between Edea and Yaounde, 21 Feb 75, collected by Thijs van den Audenaerde. RCM 54.190, 4 juv (CWs 41, 24, 24, 17 mm), Kombetiko, 5 km from Batouri, river Tanadi, 2 Feb 1976, collected by F. Puylaert. RCM 54.209, 1 F adult (CW 76.5 mm) with hatchlings, Village Aboulou, River Kom, 6 Nov 1973, collected by Thijs van den Audenaerde. ZIM K13556, 1 specimen, (CW 55 mm) Elephantense, 3 Sep 1904, collected by Richard Rohde; ZIM K3547, 1 M immature (CW 47 mm), 1 F immature (CW 63 mm), Bipindihof, near Kribi, collected by G. Zenker, 11 Jul 1914. ZIM K22517, 1 M immature (CW 56.6 mm), Brutu, collected by Prof. Vogel, Feb 1963. ZIM K 27888, 1 M adult (CW 82.5 mm), collected by Prof. Vogel 1962/1963. ZIM K27889, 1 M adult (CW 100.3 mm), Brutu, collected by Prof. Vogel, Feb 1963. ZIM K35456, 3 M (CW 36.8, 46.4, 36.4 mm), 1 F (CW 64.8 mm), Bibundi, together with *S. aubryi* (1 M CW 40.9 mm) and *S. granulatus* (1 F CW 25.7 mm), collected by Director Max. Retzlapp, 7 Sep 1909. ZMB 8235, Lake Barombi, collected by Zenker, Cameroon expedition. ZMB 9012, 1 M, Yaounde, collected by Zenker. ZMB 10024, 2 M, 1 F, Victoria, collected by Preuss. ZMB 10358, Bipindi, collected by Zenker. ZMB 10362, 1 specimen, Bipindi, collected by Zenker. ZMB 20201, 1 F, Ossidinge, collected by Mansfield. ZMB 11093, 1 specimen, Bipindi, collected by Zenker. ZMB 11094, 1 specimen, Bipindihof, collected by Zenker. ZMB 12287, 1 specimen, Lolodorf, collected by Lt. Jakob. ZMB 13433, 1 specimen, Bipindihof, collected by Zenker. ZMB 14566, 1 specimen, Bipindihof, collected by Zenker. ZMB 15183, 1 M, 1 F, Johann Albrechtshöhe, collected by Conradt. ZMB 17521, 1 specimen, collected by Dr. Escherich. ZMB 18389, 1 specimen, zoological garden, collected by Zenker. ZMB 18724, 1 M, Buala grassland 1200 m, near river Sanga, collected by Dr. J. Elbert, 11 Jan 1914. ZMB 21309, 3 M, Yaounde, collected by Prof. Haberer. ZMB 21310, 1 specimen, Bipindi, collected by Zenker. ZMB 21314, 1 M, 1 F, Johann Albrechtshöhe (modern name unknown, 4°40'N, 9°20'E) collected by Conradt. GABON: NHM, 1908.6.2–21, Abanga river (Ogoué river). RCM 55.001, 1 adult, Yeno, river Ogoulou, 1976, collected by A. C. Radda. RCM 55.175, 1 juv, 40 km

nach Tchi bauga richtung N'debde, 1980, collected by E. Purzl. AMNH 30007, Lac de Franceville, French Congo (=Gabon) M. de Brazza, in exchange Paris museum. ZAIRE: RCM 51.461, 2 M adults (CWs 100, 95 mm), Lower Congo: Ganda-Sundi, 27 Mar 1964, collected by Dr. A. Fain. RCM 51.487, 1 immature, Congo, Bas-Congo, river Bangu-Bangu, km 53 road Boma/Tshela to Cameroon, 1964, collected by J. Menliuberg. RCM 51.488, 2 M adults (CWs 108, 106 mm), 1 F adult (CW 82 mm) with hatchlings, 1 F immature (CW 73 mm), Lower Congo, Mayumbe, Ganda Sundi, river Shiloango, Mar 1964, collected by Dr. A. Fain. RCM 51.489, 10–15 juv, Congo: Mayumbe, Mar 1968, collected by Dr. A. Fain.

Diagnosis.—Terminal segment of gonopod 1 thin and needlelike, subterminal segment of gonopod 1 slim. Carapace very flat (CH/CL = 0.43). Postfrontal crest smooth, almost straight, spanning entire carapace, meeting anterolateral margins at epibranchial teeth; posterior surface of carapace in cardiac and branchial regions with patches of raised circular blisters, laterally with fields of raised short lines; semicircular, cardiac, and urogastric grooves very deep. Proximal region of pollex of propodus of major cheliped with large, conspicuously flattened tooth. Epibranchial tooth small, about half size of intermediate and exorbital teeth; exorbital tooth large; intermediate tooth large, triangular, blunt, as big as exorbital tooth. Anterolateral margin smooth behind epibranchial tooth. Largest species in Africa, growing up to CW 113 mm, pubertal molt between CW 70–75 mm.

Type Locality.—Gabon.

Distribution.—*Sudanonautes africanus* occurs in the coastal rain-forest regions of Nigeria and Central Africa. *Sudanonautes africanus* is found in Nigeria only in the south, to the east of the river Niger; this species is not known from the rest of the West African region (from western Nigeria to Senegal). In Central Africa, *S. africanus* occurs in south Cameroon, Gabon (rivers San Benito, Ogoué, Alima), Congo, and Zaire (only the lower reaches of the river Zaire basin). It is likely that this species is also found in Equatorial Guinea and Cabinda. Literature records of *S. africanus* from Klouto Mountains, Togo (Bott, 1959; Monod, 1977, 1980), from Mt. Nimba, Guinea (Bott, 1959), and from Côte d'Ivoire (Bertrand, 1979; Monod, 1977, 1980) are incorrect. Material from these localities described by

these authors, which was placed in museum collections, was examined in the present study. The specimens from Togo and Côte d'Ivoire belong to *S. aubryi* (H. Milne Edwards, 1853), and those from Guinea belong to *Liberonautes latidactylus* (de Man, 1903).

Rathbun's (1900) report of *S. africanus* in Liberia (rivers of Liberia (de Man); Mount Coffee, Liberia (O. F. Cook, USNM)) is doubtful. De Man (1903) subsequently described his specimens from Liberia as *Liberonautes latidactylus* (de Man, 1903). I have examined a mature male fresh-water crab (CW 62.5 mm) from Mount Coffee, Liberia, collected by M. J. Cook and G. N. Collins, which was donated to the MCZ by the New York State Colonization Society. The specimen is clearly *L. latidactylus*. As further circumstantial evidence, I have made regular collections of fresh-water crabs from all parts of Liberia for more than 10 months, and I have also seen a great deal of material from Liberia in museum collections. I have never once encountered a specimen of *S. africanus* from Liberia.

Description

The following description is based on an adult male (CW 83, NMU 9.IV.1983, Figs. 1a-j, 2a-i) from Nigeria.

Size.—Measurements given in Table 1.

Carapace (Fig. 1a, b).—Carapace ovoid, widest in anterior third (CW/CL 1.38), very flat (CH/CL 0.43), semicircular, urogastric, cardiac grooves very deep; cervical, transverse branchial grooves present but weak. Front bilobed, indented, anterior margin curving down, relatively narrow, less than one-third carapace width (FW/CW = 0.30). Posterior surface of carapace with patches of raised circular warts, laterally becoming fields of raised short ridges. Postfrontal crest smooth, spanning entire carapace, consisting of fused epigastric, postorbital crests, almost straight in epigastric regions, curving forward behind orbits to meet anterolateral margins at epibranchial teeth; midgroove on postfrontal crest short, forked at posterior end. Exoorbital tooth blunt, large, intermediate tooth triangular, same size as exoorbital tooth, epibranchial tooth small, low. Anterolateral margin smooth (slightly serrated when viewed under magnification),

slightly raised; continuous with posterolateral margin. Posterior margin about two-thirds as wide as carapace width.

Fields of conspicuous granules in suborbital, pterygostomial regions. Each flank with 2 sutures, 1 longitudinal, 1 vertical, dividing flank into 3 parts (Fig. 1b). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning medially at lower margin of orbit, curving backward across flank. Short vertical suture dividing suborbital region from subhepatic region marked by row of small rounded granules (Fig. 1b); suture beginning just beneath epibranchial tooth, directed forward beneath intermediate tooth, then curving down to meet longitudinal suture. First transverse groove on sternum (between sternal segments 2 and 3) complete; second groove (between sternal segments 3 and 4) consisting of 2 small notches at sides of sternum (Fig. 1c). Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long, plumose flagellum on exopod of third maxilliped (Fig. 1d); ischium of third maxilliped smooth, with faint vertical groove (Fig. 2d). Mandibular palp 2-segmented; terminal segment single, undivided, fringed with hairs, longest at junction between segments (Fig. 2a-c). Segments 1-6 of abdomen 4-sided, last segment triangular, sides indented, rounded at distal margin (Fig. 1e); segment 3 broadest, segments 4-7 tapering inward (Fig. 1e).

Chelipeds (Fig. 1f-i, k).—Unequal, right longer, higher than left. Dactylus of right cheliped slender, not arched in subadult specimens, fingers enclosing long interspace when closed, palm of propodus swollen; proximal region of fingers of digits of right cheliped with 5 large teeth (lower digit), 3 large teeth (upper digit), both fingers with 3 or 4 larger pointed teeth, interspersed with series of smaller pointed teeth along their lengths (Fig. 1f, g). In very large adults, dactylus of right cheliped with very arched fingers enclosing oval interspace when closed, palm of propodus very swollen; proximal region of both fingers of digits of right cheliped each with large flat tooth (fused proximal teeth), rest of fingers with series of smaller pointed teeth along their lengths (Fig. 1k). Inferior margins of merus with rows of

Table 1. Means (\pm SE) of ratio of carapace width (CW), carapace height (CH), front width (FW), and body size (CL) of adult *Sudanonautes africanus* compared to the adults of five closely related species of *Sudanonautes* from Nigeria and Central Africa.

	CW/CL $\bar{x} \pm \text{SE}$	CH/CL $\bar{x} \pm \text{SE}$	FW/CL $\bar{x} \pm \text{SE}$
<i>Sudanonautes africanus</i>	1.38 \pm 0.01 (N = 26)	0.43 \pm 0.003 (N = 14)	0.36 \pm 0.004 (N = 15)
<i>Sudanonautes aubryi</i> (N = 63)	1.37 \pm 0.01	0.52 ^a \pm 0.01	0.38 ^a \pm 0.002
<i>Sudanonautes floweri</i> (N = 65)	1.52 ^a \pm 0.01	0.61 ^a \pm 0.01	0.38 ^a \pm 0.003
<i>Sudanonautes granulatus</i> (N = 33)	1.42 ^b \pm 0.01	0.51 ^a \pm 0.01	0.41 ^a \pm 0.01
<i>Sudanonautes chavanesii</i> (N = 10)	1.37 \pm 0.01	0.42 \pm 0.01	0.39 ^a \pm 0.01
<i>Sudanonautes faradjensis</i> (N = 22)	1.36 \pm 0.01	0.41 \pm 0.01	0.37 \pm 0.01

Proportion significantly different from that of *S. africanus*: ^a = $P < 0.001$; ^b = $P < 0.01$; ^c = $P < 0.05$.

small teeth, cluster of granules surrounding larger pointed tooth at distal end. Inner margin of carpus of cheliped with 2 large pointed teeth, second half size of first (Fig. 1h, i). Left cheliped similar to right, but smaller in all respects (Fig. 1g). Walking legs 2–5 (pereiopods = P) slender (Fig. 1j), P4 longest, P5 shortest. Posterior margin of propodus of P2–5 serrated, dactyli of P2–5 tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus of P5 shortest of 4 legs (Fig. 1j). Stridulating apparatus associated with coxae of P2.

Gonopods.—Terminal segment of gonopod 1 very slender, long (two-thirds as long as subterminal segment), almost straight continuation of subterminal segment, curving outward only slightly, tapering to pointed tip, longitudinal groove visible from caudal and superior views (Fig. 2d, f, g), not visible from cephalic view (Fig. 2e). Subterminal segment of gonopod 1 very slim (Fig. 2d, e), with raised flap extending halfway across segment in distal part, tapering diagonally to junction with terminal segment, forming roof of chamber for gonopod 2; subterminal segment beneath flap forming lower floor of chamber for gonopod 2 (Fig. 2d). Gonopod 2 (Fig. 2h) shorter than gonopod 1 (reaching only to junction between last 2 segments of gonopod 1). Terminal segment gonopod 2 extremely short, only one-fifteenth as long as subterminal segment, sides folded inward to form spoon-shape, tip rounded (Fig. 2i). Subterminal segment gonopod 2 widest at

base, then tapering sharply inward, forming long, thin, pointed, upright process supporting short terminal segment; rounded collar at junction between terminal segment and subterminal segment.

Adult females.—Right, left chelipeds same proportions as male of same size, unequal in both length, height. Mature female abdomen very wide reaching coxae of P2–5. Segments of female abdomen 4-sided, becoming gradually longer distally, 1–5 becoming gradually wider, widest at groove separating segments 4, 5; segment 6, telson together forming near semicircle.

Growth (Fig. 3a, b, Table 1).—Carapace dimensions given in Fig. 3a, relative proportions in Fig. 3b, Table 1. Sexual maturity judged by development of female abdomen; abdomen of mature females overlapping bases of coxae of walking legs, pleopods broad, hair-fringed. Pubertal molt, from pubertal stage to sexual maturity, occurring between CW 70–75 mm. Largest known specimen (male from Cameroon) CW 113.5 mm. Hatchlings in March (Zaire), April (Nigeria), and November (Cameroon). Dimensions of carapace varying with age (Fig. 3a). Relative width of carapace (in relation to carapace length, CW/CL) increasing with age; CW/CL of adults significantly wider ($P < 0.001$) than that of juvenile and pubescent animals (Fig. 3b). Width of frontal margin (FW/CL) decreasing with age; that of juvenile and pubescent animals significantly wider ($P < 0.001$) than that of adults

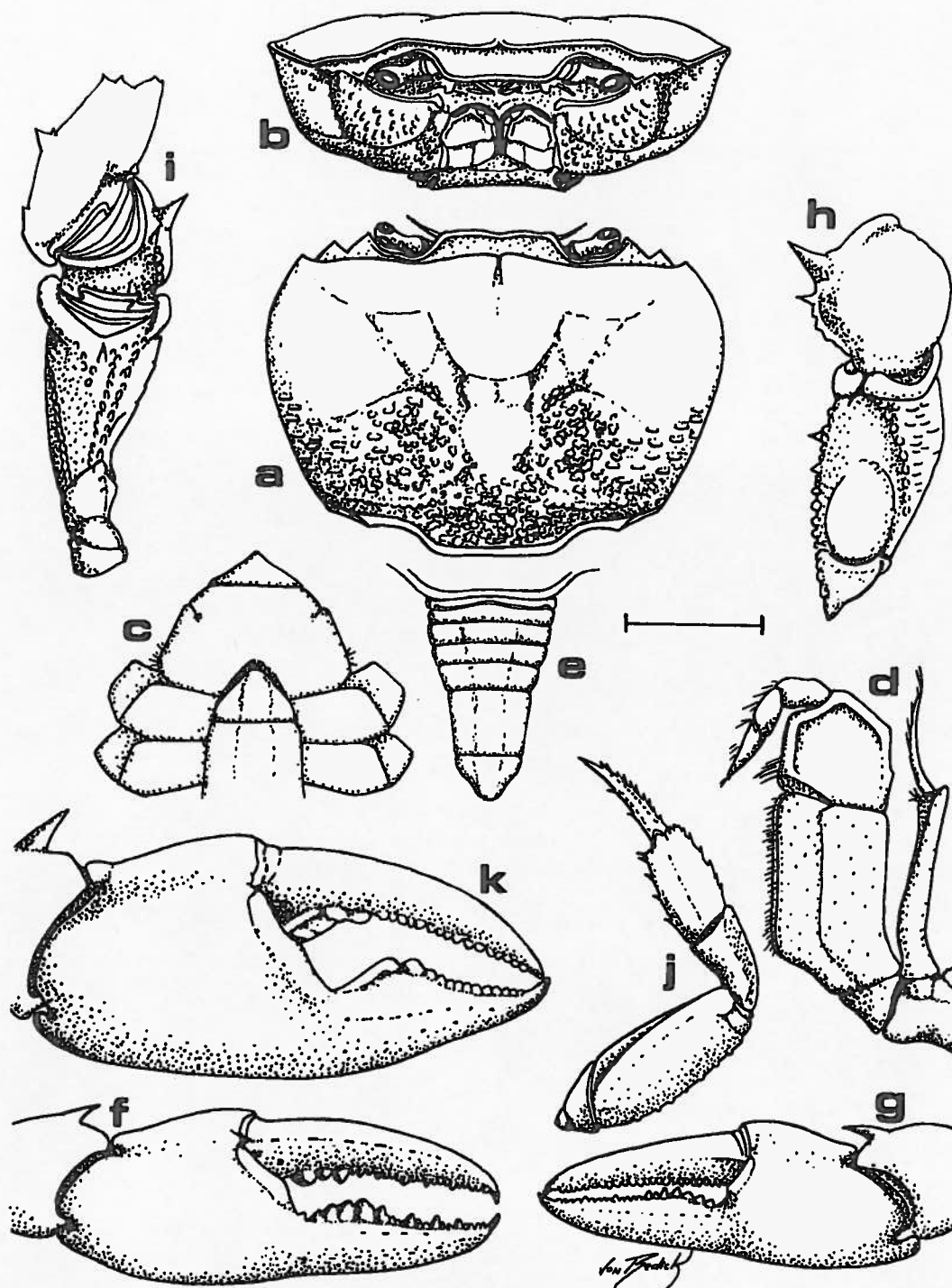


Fig. 1. *Sudanonautes africanus*, a-j, adult male (CW 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983), k, adult female (CW 108 mm) from tributary of the river Ikpan, Cross River State, Nigeria (NMU 5.IV.1983). a, whole animal, dorsal aspect; b, carapace, frontal aspect; c, sternum; d, left third maxilliped; e, abdomen; f, right cheliped, frontal view; g, left cheliped, frontal view; h, carpus and merus of right cheliped, superior view; i, carpus and merus of right cheliped, inferior view; j, left pereiopod 2; k, right cheliped, frontal view. Scale bar equals 20 mm (c, f-k), 10 mm (d), 16 mm (a, b, e).

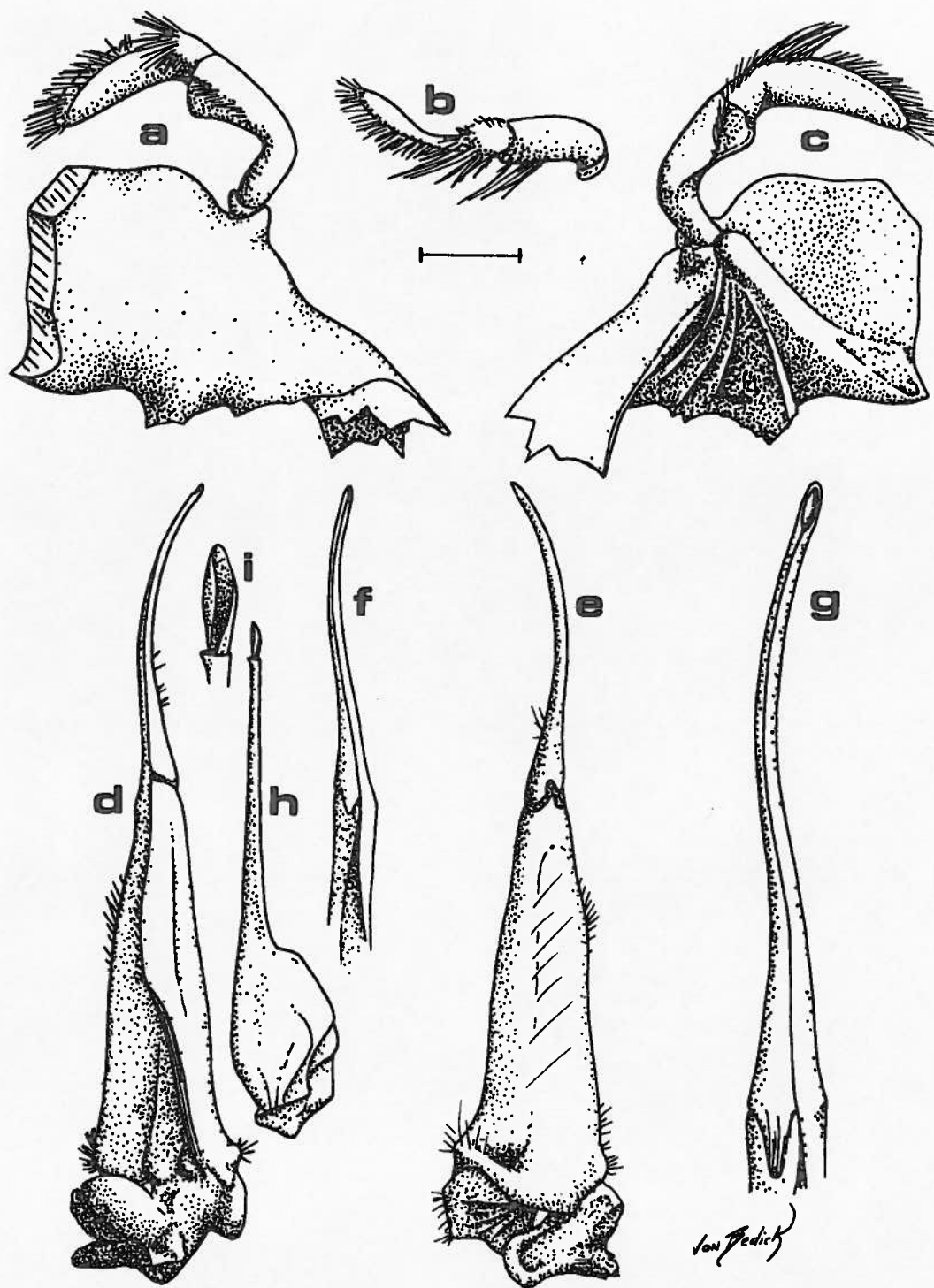


Fig. 2. *Sudanonautes africanus*, adult male (CW 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983). a, left mandible, anterior view; b, left mandible, superior view; c, left mandible, posterior view; d, left gonopod 1, caudal view; e, left gonopod 1, cephalic view; f, terminal segment of left gonopod 1, superior view; g, detail of terminal segment of left gonopod 1, superior view; h, left gonopod 2, caudal view; i, left gonopod 2, caudal view, detail of terminal segment. Scale bar equals 3 mm (a–f), 1.5 mm (g), and 1 mm (i).

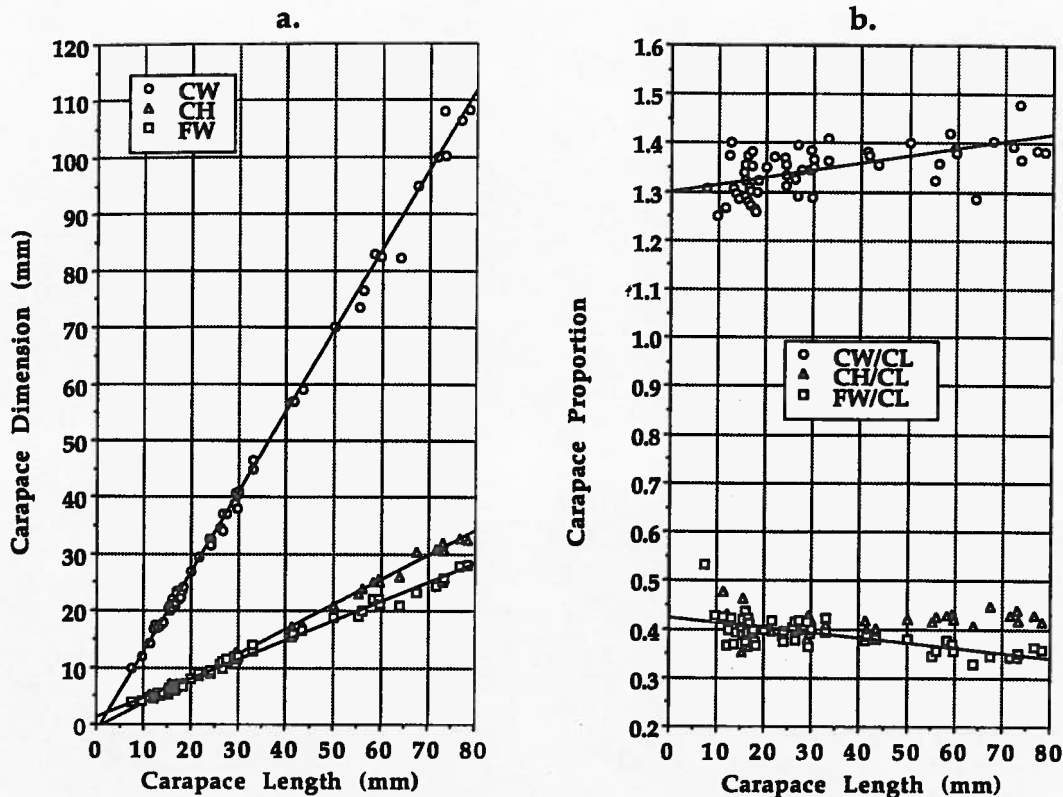


Fig. 3. Comparisons of 59 specimens of *Sudanonautes africanus*. a, dimensions of carapace (CW, CH, FW) compared to body size (CL), r values (all at $d.f. = 58$) indicate highly significant correlation ($P < 0.001$) between size classes. b, relative proportions of carapace height (CH/CL) compared to body size (CL), r values (all at $d.f. = 58$) indicate no significant correlation ($P > 0.05$) between size classes; relative proportions of carapace width (CW/CL) and front width (FW/CL), r values (all at $d.f. = 58$), indicate a highly significant correlation ($P < 0.001$) between size classes

(Fig. 3b). Relative height of carapace (CH/CL) not increasing with age; that of adult *S. africanus* not significantly higher ($P > 0.05$) than CH/CL of juvenile and pubescent animals. Shape of gonopod 1, chelipeds changing as crabs grow older. Terminal segment of gonopod 1 of subadults (CW 25–70 mm) almost straight; right and left chelipeds of subadults even-sized, palms not inflated, cutting edges meeting, not enclosing space.

Color.—(Living adult from Cross River State, Nigeria). Dorsal carapace and post-frontal crest dark brown black, flanks paler brown; eyestalk dorsal brown, ventral white, cornea black; sternum white-cream, abdomen white. Arthrodistal membranes between joints of chelipeds and pereopods bright red; ventral surface of chelipeds purplish greenish brown; pereopods and chelipeds brown dark green.

Ecological Notes

Sudanonautes africanus is restricted to the more humid areas of the coastal rain-forest belt from southeast Nigeria to lower Zaire. *Sudanonautes africanus* is capable of breathing air, and is often found on land at night. The species is common in streams and rivers draining mature forest, and also digs burrows near waterways. *Sudanonautes africanus* occurs in a range of permanent aquatic habitats from large rivers and small streams (with both fast and slow flowing water) to ponds. This crab also occurs in temporary water sources, such as drainage culverts and ditches. Most aquatic habitats were found to be shaded by overhanging climbing palms or by emergent vegetation.

Streams in Cross River State, Nigeria, ranged in size from 1–20 m wide and from

10–40 cm deep with clear, clean, well-oxygenated water. Streams draining lowland forest had a water temperature of around 26°C. Here, slow-flowing water was interspersed with stretches of faster, riffing water. The substrata of stream beds included grey sandy silts, sand, gravel, sand and gravel, stones, rounded grey boulders (10 by 10 cm), mudstone, and yellow-brown clay. In stretches where water was moving rapidly, *S. africanus* was found under stones and boulders. In stretches where water was flowing slowly, crabs were found under debris, leaf and stick jams, dead wood, and accumulations of fallen leaves. The species remains in human-altered rain-forest areas, such as mature oil palm plantations, burnt plantations, farmland, and secondary growth forest.

Juvenile and middle-sized crabs were most commonly found in streams and rivers, while adult specimens (CW 70 mm and above) tended to be more terrestrial in habit. Adult *S. africanus* dug burrows in stream banks, and burrow warrens were most conspicuous around well-shaded small streams near main rivers (Disney, 1971). Adult *S. africanus* spend the daylight hours either in water or in their burrows. At night, crabs often come out on land and forage on the forest floor.

Comments

Reports of *S. africanus* from the West African region west of the river Niger in Nigeria are based on incorrectly identified material. For example, the description of growth (Ejike, 1972) and salt and water balance (Lutz, 1969) in populations of freshwater crabs from Ibadan, Nigeria, actually refer to *S. aubryi*, not *S. africanus*. Similarly, reports of *S. africanus* in Togo (Bott, 1959; Monod, 1980) and in Côte d'Ivoire (Bertrand, 1979) refer to *S. aubryi*, not *S. africanus*. The specimens from Guinea identified by Bott (1959) and by Monod (1980) as *S. africanus* actually belong to *Liberonautes latidactylus* (de Man, 1903). Furthermore, parasitologists working on human paragonimiasis in Nigeria and Cameroon wrongly identified *S. africanus* as *S. aubryi* (see Voelker and Sachs, 1977, fig. 1), and *S. aubryi* as *S. africanus* (see Voelker et al., 1975, fig. 6).

Comparisons

Sudanonautes africanus is the largest species of fresh-water crab in Africa, growing up to CW 113.5 mm, with a pubertal molt between CW 70–75 mm. Specimens of all other species in the genus would be fully mature at CW 65 mm or above.

Sudanonautes africanus is most likely to be confused with other large species occurring in the rain forest zones of Central Africa, such as *S. chavanesii* and *S. faradjensis* (Rathbun, 1921). *Sudanonautes africanus* can be distinguished from *S. chavanesii* by the postfrontal crest. In *S. africanus* this forms an unbroken line across the carapace (Fig. 1a), whereas in *S. chavanesii* the crest has a distinct notch behind the upper orbital margin (Cumberlidge, 1995). In addition, the terminal segment of gonopod 1 of *S. africanus* is long, thin, and only slightly curved (Fig. 2d, e), whereas that of *S. chavanesii* is relatively wide and curves distinctly outward (Cumberlidge, 1995). Finally, the epibranchial tooth of *S. chavanesii* is distinct, sharp, and pointed (Cumberlidge, 1995), while that of *S. africanus* is small, low, and blunt (Fig. 1a, b).

The holotype of *S. faradjensis*, an adult male (CW 71.5, CL 51.0) from Faradje, Zaire (AMNH 3346), was examined and compared with *S. africanus*. *Sudanonautes africanus* can be distinguished from *S. faradjensis* by the anterolateral margin; that of *S. africanus* is smooth, whereas in *S. faradjensis* there are rows of sharp teeth on the anterolateral margin behind the epibranchial tooth. In addition, the epibranchial tooth of *S. africanus* is small and low, whereas that of *S. faradjensis* is sharp and pointed.

There are a number of characters which distinguish *S. africanus* from the three other species of fresh-water crabs that host the human lung fluke in Nigeria and Central Africa. For example, the carapace of *S. africanus* is significantly flatter ($P < 0.001$) than these three species (Table 1), and the carapace of *S. africanus* is rough with warty patches and ridges in the posterior region, and deep urogastric and cardiac grooves (Fig. 1b). The following additional characters can be used to distinguish *S. africanus* from these species.

The terminal segment of gonopod 1 of *S.*

aubryi is stouter and more curved than that of *S. africanus*, which is thin and needlelike (Fig. 2d-f). In addition, the postfrontal crest of *S. aubryi* meets the anterolateral margin behind the epibranchial tooth, while that of *S. africanus* meets this margin at the epibranchial tooth.

Sudanonautes africanus can be distinguished from *S. floweri* by the terminal segment of gonopod 1; that of *S. floweri* has a raised cephalic lobe, and a distinct longitudinal groove in dorsal view (see Capart, 1954, fig. 21), while that of *S. africanus* lacks these features (Fig. 2d-f). In addition, the outer margin of the subterminal segment of gonopod 1 of *S. floweri* is conspicuously broadened (see Capart, 1954, fig. 21), while that of *S. africanus* is slim. The sternum of *S. floweri* has raised ridges at the points where the chelipeds insert, while *S. africanus* lacks these sternal ridges (Fig. 1c). The carapace of *S. floweri* is significantly ($P < 0.001$) wider (CW/CL *S. floweri* = 1.51, *S. aubryi* = 1.37) than that of *S. africanus* (Table 1). Finally, the carapace and postfrontal crest of *S. floweri* are uniformly red brown with a contrasting yellow postfrontal crest, while these features are green brown in *S. africanus*.

Sudanonautes africanus can be distinguished from *S. granulatus* by the terminal segment of gonopod 1; that of *S. granulatus* has a raised cephalic lobe and a distinct longitudinal groove (Cumberland, 1993a), while that of *S. africanus* lacks these features (Fig. 2d-f). Furthermore, the carapace of *S. granulatus* is significantly ($P < 0.001$) wider than that of *S. africanus* (CW/CL *S. granulatus* = 1.41, *S. africanus* = 1.38, Table 1). Finally, the chelipeds of *S. granulatus* are brick red yellow, and the arthroal membranes are brown yellow (Cumberland, 1993a), while the chelipeds of *S. africanus* are green brown, and the arthroal membranes bright red.

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Address: Department of Biology, Northern Michigan University, Marquette, Michigan 49855, U.S.A.